

Jewels on the go: exotic buprestids around the world (Coleoptera, Buprestidae)

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Abstract

Buprestidae (Coleoptera: Buprestoidea) is one of the three wood-borer beetle groups of major phytosanitary interest worldwide, together with Cerambycidae and Scolytinae (Curculionidae). As in other beetle families, some buprestid species have been unintentionally or intentionally introduced around the world, in some cases causing significant environmental and economic damage in the invaded territories. Despite the phytosanitary relevance of the Buprestidae, information regarding the identity of exotic buprestids, their biogeographic areas of origin, introduction pathways, and larval host plants, have remained scattered in the literature. Our objective was to summarize much of the existing knowledge on these topics in the present paper. Our analysis resulted in a list of 115 exotic buprestids worldwide, representing introductions both within and between biogeographic realms and corresponding to less than 1% of the known buprestid species worldwide. Invasiveness does not seem to be linked to their larval host plant preferences, as introduced species utilize 158 plant genera in 70 plant families and are equally represented in all feeding guilds (monophagous, oligophagous, and polyphagous). As trade of plants or plant parts can serve as a pathway for future introductions, the information reported in this review can help in pest risk assessment.

Keywords

Biodiversity, exotic species, invasive alien species, jewel beetles

Introduction

Buprestidae Leach, 1815 (Coleoptera: Buprestoidea), commonly known as jewel beetles, include more than 15,000 described species distributed in all continents except Antarctica (Bellamy 2008). The family includes six subfamilies, namely Agrilinae, Buprestinae, Chrysochroinae, Galbellinae, Julodinae, and Polycestinae, (Bellamy 2003).

All Buprestidae are phytophagous and generally oligophagous (i.e., associated with a single plant family) as both adults and larvae (Curletti 1994). Buprestid larvae develop in both living and dead plant tissues; most species are internal feeders, boring or mining in roots, stems, branches, and leaves of both woody plants and herbaceous plants (Bellamy and Volkovitsh 2005), while only Julodinae possess soil-dwelling larvae that feed externally on roots (Kolibáč 2000).

Many buprestids, especially the wood-boring species, select dead, dying, or stressed plants for oviposition (Chamorro et al. 2015); however, some species are capable of infesting or even prefer healthy living hosts (Carlson and Knight 1969). This last group can have an important economic impact on human activities because it includes pests in orchards and tree plantations (Bonsignore et al. 2008; Hashim et al. 2018; Dawadi et al. 2019). Furthermore, buprestids can have substantial negative impacts on the natural ecosystems during outbreaks (Coleman et al. 2012; Muilenburg and Herms 2012; Sallé et al. 2014; Vuts et al. 2016; Haack and Petrice 2019).

The cryptic nature of most buprestid larvae, being hidden in woody tissues and, for some species, their slow larval development due to feeding in nutrient-poor xylem (Haack and Slansky 1987), has allowed multiple species to be transported in wood products and introduced to areas far from their place of origin. Much of this dispersal has been human-mediated and related to trade (Wu et al. 2017). One of the earliest accounts deals with the introduction of *Chalcophora detrita detrita* (Klug, 1829) from the Middle East to Southern Italy by the Etruscans or the Maritime Republics (from 1000 to 2000 years ago; Biagioni et al. 2015). However, since the end of the nineteenth century the introduction rate of exotic buprestids worldwide has substantially increased in similar fashion to many other invasive forest insects (Aukema et al. 2010; Chamorro et al. 2015; Hoebeke et al. 2017; Bozorov et al. 2018; Jendek et al. 2018; Roques et al. 2020; Volkovitsh et al. 2020).

Buprestidae have taken advantage of globalization with the opening of new trade routes and the increase in the number and speed of movement of goods and people (Pyšek and Richardson 2010). In some cases, species such as *Agrilus planipennis* Fairmaire, 1888 (hosts: *Chionanthus* and *Fraxinus* [main host]), *A. mali* Matsumura, 1924 (hosts: *Cydonia*, *Emmenopterys*, *Malus* [main], *Prunus*, *Pyrus*, *Sorbus*), and *Aphanisticus cochinchiniae seminulum* Obenberger, 1929 (hosts: *Saccharum*, *Tripsacum*) have become invasive, causing significant damage in urban and natural forests and agriculture, and often requiring significant investments for monitoring and control (Hespenheide 2007; Bauer et al. 2008; Jones et al. 2013; Volkovitsh et al. 2020). Consequently, Buprestidae is one of the Coleoptera families of major silvicultural interest worldwide (Maynard et al. 2004; Inghilesi et al. 2013; Haack et al. 2014; MacQuarrie et al. 2020).

Given this condition, great efforts have been made in the last few decades to identify the main entry pathways, and to develop and implement early detection programs, effective monitoring strategies, and new tools for species identification (Meurisse et al. 2019; Poland and Rassati 2019). To date, however, little has been summarized about the main patterns of buprestid introductions worldwide, their taxonomic affinities, and their biogeographic origins.

The purpose of this article is to provide a comprehensive review of natural and human-assisted translocation of buprestid species among and within various biogeographic realms, describe the contribution of each realm and buprestid subfamily to this exchange of species, and provide the first comprehensive list of all introduced Buprestidae worldwide from the mid-1800s to present. Furthermore, a list of host plant associations at the genus and family level is provided, with an indication of the host range of each buprestid species. Our general aim is to provide information that can be used in pest risk assessment and invasion ecology.

Methods

In order to compile and then review the literature on exotic Buprestidae, we performed reiterated research in Google Scholar through the use of keywords such as “Buprestidae,” “introduced,” “exotic,” and “alien” and then integrated with the Boolean operators AND, OR, NOT and the use of “ ” for specific word combinations. We also obtained a considerable amount of literature that was not available in Google Scholar thanks to the support of many colleagues and buprestid specialists. Screening of the literature collected was done following the PRISMA approach and only the papers retained are cited in the Suppl. material 1 and were used for the analysis (Moher et al. 2009). The resulting reference library included papers in Chinese, English, French, German, and Italian.

In the analysis, we considered only those publications where buprestids were identified to species or subspecies level, and for those records published between 1850 and December 2020. In the taxonomic discussion, we did not consider the rank of subgenus. In particular, the non-native status of a given species was evaluated for its consistency throughout the reviewed literature; in case there was only a single reference publication and in the absence of any further information, the non-native status of a species was considered as valid. For each species included in the present research, we considered the most recent and comprehensive publication highlighting and explaining the non-native status as a key reference. For those buprestid species for which the literature was limited, we referred to the original faunistic record published. A full list of the Buprestidae species, associated with the reference literature, is provided in Suppl. material 1.

Where the origin of a given taxon could not be assigned to a single biogeographic region, every possible area of origin was considered. The world's biogeographic areas considered in this paper generally follow the interpretation and categorization provided by Löbl and Löbl (2016).

At times it was difficult to know if an insect was firmly established in a new area or was simply intercepted at a port of entry, because papers varied in terminology and detail. In our dataset, when considering the species status, we have generally adopted the following categorization: A) Neonative: species native to a continent but introduced into regions other than the native ones either through natural spread indirectly favored by human activities (climate change, habitat change) or through accidental human-mediated introductions; B) Established: non-native species that sustain self-replacing populations over several life cycles (inclusive of single specimens collected in the wild away from potential entry points); C) Invasive: a non-native species established in natural or semi-natural ecosystems or habitat, which has impact and threatens native biological diversity; D) Intercepted: insects detected during inspection procedures or similar situations where no reproducing population is known to occur; E) Intentionally introduced: species that have been actively introduced in areas other than their native range with a specific purpose, such as biological control of invasive plants; F) Unclear: all species for which the status is unclear (e.g., apparently extinct adventive populations, species described in areas where that specific genus does not occur, species record vague without any specific detail, mislabeling and misidentification).

Data collected were organized in an Excel spreadsheet including the following information, organized by columns: subfamily, tribe, genus, species (full name plus author), biogeographic region of origin, biogeographic region of detection, status, and host plants. Detection region and host plant were associated with a specific column called references, which included all relevant information used to recover the data. Each species could have multiple entries (rows) in cases of multiple introduction events in different biogeographic areas, or in situations where the origin of the species was not reducible to a single biogeographic region. In the case of single introductions of widely distributed species in which it was clear the biogeographic region of origin of the insects, we considered only the record for that specific region. The taxonomy of plant genera and families used in the paper is based on the information available on the “Plants of The World Online” database (<https://pwo.science.kew.org/>). Analyses and graphics were realized using the R software (version 4.1.2).

Host plant preference was defined in the categories: monophagous (for buprestids feeding only on plant species of the same genus), oligophagous (buprestids feeding on different plant genera within the same host family), polyphagous (buprestids feeding on plant species from different host families).

Results

Faunistic part

Our literature review identified 162 events of buprestid introductions among and within biogeographic regions that involved 115 distinct taxa (Suppl. material 1). The taxa included 44 species in the subfamily Agrilinae (tribes Agrilini, Aphanistiini, Coraebini, and Tracheini) (Table 1), 51 species of Buprestinae (tribes Anthaxiini,

Buprestini, Chrysobothrini, Curidini, Melanophilini, and Nascionini) (Table 2), 16 species of Chrysochroinae (Chalchophorini, Chrysochroini, Dicercini, Sphenopterini, Paraleptodemini, and Poecilonotini) (Table 3), and 6 species of Polycestinae (tribes Acmaeoderini, Polycestini, Prospherini and Ptosimini) (Table 4). No species of the subfamilies Galbellinae and Julodinae were recorded as introduced. The revision of all published records revealed that the buprestid species involved in introductions either within or between biogeographical realms constitute only 0.76% of all known buprestid species worldwide.

The analysis showed that the introduction of exotic Buprestidae included all biogeographic realms (with the obvious exclusion of the Antarctic realm), including introductions both among and within the realms (Fig. 1). In addition, our analysis revealed that the Nearctic and Palearctic bioregions contributed the greatest number of introduced species (90 in total) and also the most distinct introduction events (72.4% combined). The realm that was the source for the highest number of buprestids introduced elsewhere was the Palearctic, with 52 out of approximately 2,500 native species (2.1%), followed by the Nearctic (38 out of ~800; 4.8%), the Indomalayan (13 out of ~2,800; 0.5%), the Neotropical (13 out of ~3,700; 0.4%), the Australasian (10 out of ~1,600; 0.6%), the Afrotropical (7 out of ~3,800; 0.2%), and the Oceanian (2 out of ~70; 2.9%). The analyses between the number of buprestid species per biogeographic realm and the number of species introduced elsewhere from each realm did not show any significant statistical relation ($t = -0.10389$, $df = 5$, $p\text{-value} = 0.9213$).

Palearctic and Nearctic were the two regions with the highest number of introduced species (Fig. 1) but, despite somewhat similar environments, climate, and flora, there were substantial differences in the patterns of inter- and intra-biogeographic realm introductions (Table 5). In the case of intra-realm introductions, Palearctic and Nearctic showed a similar number of species (23 vs 20) despite the fact that the genera contributing to more than 50% of total introductions were, at least in part, different: *Agrilus* (9 species) and *Buprestis* (4 species) in the Palearctic, and *Chrysobothris* (9) and *Agrilus* (6) in the Nearctic.

By contrast, when considering introductions between the two realms, it was possible to observe a strong imbalance with 9 exotic species recorded in the Palearctic compared with 25 in the Nearctic. Furthermore, Agrilinae represented the majority of the exotic buprestids in the Nearctic, while Buprestinae were dominant in the Palearctic.

With respect to all buprestid species considered introduced worldwide, we found 41 cases where the species were considered established, 43 cases as interceptions at entry points, 32 cases where the status was unclear, and 22 cases of neonative species. We also classified 13 introductions where the species became invasive, and 6 cases where species were intentionally introduced.

For the 41 cases of establishment, Buprestinae was the most represented subfamily, with 23 records subdivided among the genera *Anthaxia* (1 species), *Buprestis* (8 species), *Belionota* (1 species), *Chrysobothris* (6 species), and *Trachypterus* (1 species). Agrilinae accounted for 14 establishments, represented by 10 species of *Agrilus*, 1 *Diphucrania*, and 2 *Trachys*. The subfamilies Chrysochroinae and Polycestinae were involved in only a limited number of establishments, i.e., 1 *Steraspis*, 1 *Prospheres* and 2 *Acmaeodera*.

Table 1. Subfamily Agrilinae: species list, biogeographic realms concerned, status, and larval host plants.
* species confused with *Agrilus coxalis* Waterhouse, 1889 in the literature.

Species	Biogeographic realm		Status	Plant host genera
	origin	introduction		
<i>Agrilus angustulus</i> (Illiger, 1803)	Palearctic	Palearctic	Unclear	<i>Corylus, Ostrya</i> (Betulaceae); <i>Fagus, Castanea, Quercus</i> (Fagaceae)
<i>Agrilus anxius</i> Gory, 1841	Nearctic	Nearctic	Neonative	<i>Betula</i> (Betulaceae)
<i>Agrilus auriventris</i> Saunders, 1873	Australasian, Indomalayan	Oceanian	Invasive	<i>Citrus</i> (Rutaceae)
<i>Agrilus auroguttatus</i> Schaeffer, 1905*	Nearctic	Nearctic	Invasive	<i>Quercus</i> (Fagaceae)
<i>Agrilus bilineatus</i> (Weber, 1801)	Nearctic	Palearctic	Established	<i>Castanea, Quercus</i> (Fagaceae)
<i>Agrilus biguttatus</i> (Fabricius, 1776)	Palearctic	Australasian	Intercepted	<i>Fagus, Castanea, Quercus</i> (Fagaceae); <i>Tilia</i> (Malvaceae); <i>Populus</i> (Salicaceae); <i>Ulmus</i> (Ulmaceae)
<i>Agrilus cavatus</i> Chevrolat, 1838	Nearctic	Neotropical	Unclear	<i>Rhus</i> (Anacardiaceae); <i>Acaciella</i> (Fabaceae)
<i>Agrilus convexicollis</i> Redtenbacher, 1849	Palearctic	Palearctic	Neonative	<i>Euonymus</i> (Celastraceae); <i>Philadelphus</i> (Hydrangeaceae); <i>Fraxinus, Ligustrum, Olea, Syringa</i> (Oleaceae)
<i>Agrilus cuprescens</i> (Ménétriés, 1832)	Palearctic	Nearctic	Established	<i>Rosa, Rubus</i> (Rosaceae)
<i>Agrilus cyanenorhynchus</i> Saunders, 1873	Palearctic	Palearctic	Neonative	<i>Croton</i> (Euphorbiaceae); <i>Quercus</i> (Fagaceae)
<i>Agrilus cyanescens</i> (Ratzeburg, 1837)	Palearctic	Palearctic, Nearctic	Unclear, Established	<i>Lonicera, Symporicarpos</i> (Caprifoliaceae); <i>Rhamnus</i> (Rhamnaceae)
<i>Agrilus deraosfasciatus</i> Lacordaire, 1835	Palearctic	Nearctic	Non-native	<i>Vitis</i> (Vitaceae)
<i>Agrilus difficilis</i> Gory, 1841	Nearctic	Nearctic	Established	<i>Gleditsia</i> (Fabaceae); <i>Zanthoxylum</i> (Rutaceae)
<i>Agrilus extraneus</i> Fisher, 1933	Oceanian	Oceanian	Established	<i>Argemone</i> (Papaveraceae)
<i>Agrilus fleischeri</i> Obenberger, 1925	Palearctic	Nearctic	Intercepted	<i>Populus, Salix</i> (Salicaceae)
<i>Agrilus furcillatus</i> Chevrolat, 1835	Nearctic, Neotropical	Nearctic	Intercepted	<i>Pinus</i> (Pinaceae); <i>Zea</i> (Poaceae); <i>Coffea</i> (Rubiaceae); <i>Salix</i> (Salicaceae)
<i>Agrilus graminis</i> Kiesenwetter, 1857	Palearctic	Palearctic	Neonative	<i>Alnus, Corylus, Ostrya</i> (Betulaceae); <i>Euonymus</i> (Celastraceae); <i>Castanea, Quercus</i> (Fagaceae); <i>Acer</i> (Sapindaceae); <i>Viburnum</i> (Viburnaceae)
<i>Agrilus hyperici</i> (Creutzer, 1799)	Palearctic	Australasian, Nearctic	Intentionally introduced	<i>Hypericum</i> (Hypericaceae)
<i>Agrilus kaluganus</i> Obenberger, 1940	Palearctic	Palearctic	Neonative	<i>Corylus</i> (Betulaceae)
<i>Agrilus livens</i> Kerremans, 1892	Indomalayan	Palearctic	Unclear	<i>Citrus</i> (Rutaceae)
<i>Agrilus mali</i> Matsumura, 1924	Palearctic	Palearctic	Neonative	<i>Cydonia, Malus, Prunus, Pyrus, Sorbus</i> (Rosaceae); <i>Emmenopterys</i> (Rubiaceae)
<i>Agrilus nicolanus</i> Obenberger, 1924	Palearctic	Palearctic	Neonative	<i>Quercus</i> (Fagaceae); <i>Ulmus</i> (Ulmaceae)
<i>Agrilus occipitalis</i> (Eschscholtz, 1822)	Australasian, Indomalayan, Palearctic	Oceanian	Invasive	<i>Citrus</i> (Rutaceae)
<i>Agrilus pilosovittatus</i> Saunders, 1873	Palearctic	Nearctic	Established	<i>Wisteria</i> (Fabaceae)
<i>Agrilus planipennis</i> Fairmaire, 1888	Palearctic	Nearctic, Palearctic	Invasive, Neonative	<i>Chionanthus, Fraxinus</i> (Oleaceae)
<i>Agrilus prionurus</i> Chevrolat, 1838	Nearctic	Nearctic	Neonative	<i>Chionanthus</i> (Oleaceae); <i>Sapindus</i> (Sapindaceae)
<i>Agrilus pulchellus</i> Bland, 1865	Nearctic	Nearctic	Intercepted	<i>Chrysanthemum</i> sp., <i>Erigeron</i> (Asteraceae); <i>Amsinkia</i> (Boraginaceae); <i>Celtis</i> (Cannabaceae); <i>Quercus</i> (Fagaceae); <i>Sphaeralcea</i> (Malvaceae); <i>Allionia, Boerhavia</i> (Nyctaginaceae)
<i>Agrilus ribesi</i> Schaefer, 1946	Palearctic	Nearctic	Invasive	<i>Ribes</i> (Grossulariaceae)
<i>Agrilus sinuatus</i> (Olivier, 1790)	Palearctic	Nearctic	Established	<i>Crataegus, Malus, Prunus, Pyrus, Sorbus</i> (Rosaceae)
<i>Agrilus smaragdifrons</i> Ganglbauer, 1890	Palearctic	Nearctic	Established	<i>Ailanthus</i> (Simaroubaceae)
<i>Agrilus sulcicollis</i> Lacordaire, 1835	Palearctic	Nearctic	Established	<i>Fagus, Castanea, Quercus</i> (Fagaceae)
<i>Agrilus subrobustus</i> Saunders, 1873	Indomalayan, Palearctic	Nearctic	Established	<i>Albizia</i> (Fabaceae)
<i>Aphanisticus antennatus</i> Saunders, 1873	Palearctic	Indomalayan, Neotropical	Unclear	Not available

Species	Biogeographic realm		Status	Plant host genera
	origin	introduction		
<i>Aphanisticus cochinchiniae seminulum</i> Obenberger, 1929	Indomalayan	Nearctic, Neotropical, Oceanian	Invasive	<i>Saccharum, Tripsacum</i> (Poaceae)
<i>Coraebus andrewesi</i> Obenberger, 1922	Indomalayan, Palearctic	Neotropical	Unclear	Not available
<i>Coraebus rubi</i> (Linnaeus, 1767)	Palearctic	Palearctic	Neonative	<i>Rosa, Rubus</i> (Rosaceae)
<i>Coraebus undatus</i> (Fabricius, 1787)	Palearctic	Palearctic	Intercepted	<i>Diospyros</i> (Ebenaceae); <i>Castanea, Fagus, Quercus</i> (Fagaceae)
<i>Diphucrania viridipurpurea</i> Carter, 1924	Australasian	Palearctic	Established	Not available
<i>Hylaeogena jureceki</i> Obenberger, 1941	Neotropical	Afrotropical, Australasian	Intentionally introduced	<i>Dolichandra</i> (Bignoniaceae)
<i>Leiopleura carbonata</i> (LeConte, 1860)	Neotropical	Neotropical	Unclear	Not available
<i>Leiopleura otero</i> (Fisher, 1935)	Neotropical	Neotropical	Unclear	Not available
<i>Lius poseidon</i> Napp, 1972	Neotropical	Oceanian	Intentionally introduced	<i>Miconia, Chaetogastra</i> (Melastomataceae)
<i>Trachys minutus</i> (Linnaeus, 1758)	Palearctic	Nearctic	Established	<i>Corylus</i> (Betulaceae); <i>Sorbus</i> (Rosaceae); <i>Salix</i> (Salicaceae), <i>Ulmus</i> (Ulmaceae)
<i>Trachys troglodytiformis</i> Obenberger, 1918	Palearctic	Nearctic	Established	<i>Althea, Hibiscus, Malva</i> (Malvaceae)

Table 2. Subfamily Buprestinae: species list, biogeographic realms concerned, status, and larval host plants.

Species	Biogeographic realm		Status	Plant host genera
	origin	introduction		
<i>Anthaxia godeti</i> Gory & Laporte, 1839	Palearctic	Palearctic	Neonative	<i>Picea, Pinus</i> (Pinaceae)
<i>Anthaxia laticeps</i> Abeille de Perrin, 1900	Palearctic	Palearctic	Neonative	<i>Pinus</i> (Pinaceae)
<i>Anthaxia proteus</i> Saunders, 1873	Palearctic	Palearctic	Unclear	<i>Pinus</i> (Pinaceae)
<i>Anthaxia salicis</i> (Fabricius, 1776)	Palearctic	Nearctic	Established	<i>Castanea, Quercus</i> (Fagaceae); <i>Salix</i> (Salicaceae); <i>Acer</i> (Sapindaceae)
<i>Cobosina willineri</i> (Cobos, 1972)	Neotropical	Neotropical	Neonative	Not available
<i>Buprestis apricans</i> Herbst, 1801	Nearctic	Neotropical	Established	<i>Pinus</i> (Pinaceae)
<i>Buprestis aurulenta</i> Linnaeus, 1767	Nearctic	Australasian, Neotropical, Palearctic, Oceanian	Intercepted, Established, Unclear, Established	<i>Thuja, Juniperus</i> (Cupressaceae); <i>Abies, Picea, Pinus, Pseudotsuga</i> (Pinaceae)
<i>Buprestis dalmatina</i> Mannerheim, 1837	Palearctic	Nearctic, Palearctic	Intercepted, Neonative	<i>Pinus</i> (Pinaceae)
<i>Buprestis decora</i> Fabricius, 1775	Nearctic	Neotropical, Palearctic	Established	<i>Pinus</i> (Pinaceae)
<i>Buprestis haemorrhoidalis</i> Herbst, 1780	Palearctic	Afrotropical, Australasian, Nearctic, Neotropical, Palearctic	Unclear, Intercepted, Established, Unclear, Unclear	<i>Callitris</i> (Cupressaceae); <i>Abies, Picea, Pinus</i> (Pinaceae)
<i>Bruprestis humeralis</i> Klug, 1829	Palearctic	Palearctic	Neonative	<i>Pinus</i> (Pinaceae)
<i>Buprestis lineata</i> Fabricius, 1781	Nearctic	Australasian, Nearctic, Neotropical, Palearctic	Intercepted, Neonative, Established, Unclear	<i>Pinus</i> (Pinaceae)
<i>Buprestis maculativentris</i> Say, 1825	Nearctic	Australasian	Intercepted	<i>Abies, Picea, Pinus</i> (Pinaceae)
<i>Buprestis maculipennis</i> Gory, 1841	Nearctic	Neotropical	Established	<i>Taxodium</i> (Cupressaceae); <i>Pinus, Tsuga</i> (Pinaceae)
<i>Buprestis novemmaculata</i> Linnaeus, 1767	Palearctic	Afrotropical, Indomalayan, Nearctic, Neotropical, Palearctic	Unclear, Unclear, Intercepted, Established, Established	<i>Larix, Picea, Pinus</i> (Pinaceae)
<i>Buprestis salisburyensis</i> Herbst, 1801	Nearctic	Nearctic	Established	<i>Pinus</i> (Pinaceae)

Species	Biogeographic realm		Status	Plant host genera
	origin	introduction		
<i>Trachykele blondeli</i> Marseul, 1865	Nearctic	Australasian, Palearctic	Intercepted, Non-native	<i>Calocedrus, Chamaecyparis, Cupressus, Juniperus, Thuja</i> (Cupressaceae)
<i>Belionota prasina</i> (Thunberg, 1789)	Australasian, Indomalayan	Afrotropical, Australasian, Nearctic, Neotropical, Palearctic	Established, Intercepted, Established, Established, Intercepted	<i>Anacardium, Mangifera</i> (Anacardiaceae); <i>Delonix, Pithecellobium</i> (Fabaceae); <i>Casuarina</i> (Casuarinaceae); <i>Hopea</i> (Dipterocarpaceae); <i>Ceiba</i> (Malvaceae)
<i>Merimna atrata</i> (Gory & Laporte, 1837)	Australasian	Oceanian	Intercepted	<i>Eucalyptus</i> (Myrtaceae)
<i>Chrysobothris adelpha</i> Gemminger & Harold, 1869	Nearctic	Oceanian	Intercepted	<i>Prosopis</i> (Fabaceae); <i>Carya</i> (Juglandaceae); <i>Amelanchier</i> (Rosaceae)
<i>Chrysobothris acutipennis</i> Chevrolat, 1835	Nearctic, Neotropical	Neotropical	Established	<i>Ebenopsis, Leucaena</i> (Fabaceae)
<i>Chrysobothris affinis</i> (Fabricius, 1794)	Palearctic	Australasian	Intercepted	<i>Pistacia</i> (Anacardiaceae); <i>Alnus, Betula, Carpinus, Corylus, Ostrya</i> (Betulaceae); <i>Cornus</i> (Cornaceae); <i>Arbutus</i> (Ericaceae); <i>Cercis, Gleditsia, Robinia</i> (Fabaceae); <i>Castanea, Fagus, Quercus</i> (Fagaceae); <i>Punica</i> (Lythraceae); <i>Juglans</i> (Juglandaceae); <i>Tilia</i> (Malvaceae); <i>Ficus, Morus</i> (Moraceae); <i>Eucalyptus</i> (Myrtaceae); <i>Fraxinus</i> (Oleaceae); <i>Cedrus</i> (Pinaceae); <i>Platanus</i> (Platanaceae); <i>Crataegus, Malus, Prunus, Pyrus, Rosa, Sorbus</i> (Rosaceae); <i>Populus, Salix</i> (Salicaceae); <i>Acer</i> (Sapindaceae); <i>Ulmus</i> (Ulmaceae)
<i>Chrysobothris analis</i> LeConte, 1860	Nearctic	Nearctic	Established	<i>Rhus</i> (Anacardiaceae); <i>Celtis</i> (Cannabaceae); <i>Diospyros</i> (Ebenaceae); <i>Cercis, Ebenopsis, Haematoxylum, Leucaena, Mimosa, Parkinsonia, Prosopis</i> (Fabaceae); <i>Carya, Juglans</i> (Juglandaceae); <i>Coccobola</i> (Polygonaceae); <i>Prunus</i> (Rosaceae); <i>Citrus</i> (Rutaceae); <i>Sapindus</i> (Sapindaceae); <i>Ulmus</i> (Ulmaceae)
<i>Chrysobothris cavifrons</i> Deyrolle, 1864	Australasian	Palearctic	Intercepted	Not available
<i>Chrysobothris cerceripraeda</i> Westcott & Thomas, 2015	Nearctic	Nearctic	Unclear	Not available
<i>Chrysobothris chrysonota</i> Deyrolle, 1864	Australasian	Palearctic	Intercepted	Not available
<i>Chrysobothris costata</i> Kerremans, 1895	Oceanian	Oceanian	Invasive	<i>Intsia</i> (Fabaceae); <i>Citrus</i> (Rutaceae)
<i>Chrysobothris costifrons</i> Waterhouse, 1887	Nearctic	Nearctic	Neonative	<i>Quercus</i> (Fagaceae)
<i>Chrysobothris dorsata</i> (Fabricius, 1787)	Afrotropical, Palearctic	Palearctic	Unclear	<i>Acacia, Ceratonia</i> (Fabaceae)
<i>Chrysobothris ellyptica</i> Deyrolle, 1864	Australasian	Palearctic	Intercepted	Not available
<i>Chrysobothris femorata</i> (Olivier, 1790)	Nearctic	Australasian, Oceanian, Palearctic	Intercepted	<i>Liquidambar</i> (Altingiaceae); <i>Carpinus</i> (Betulaceae); <i>Celtis</i> (Cannabaceae); <i>Diospyros</i> (Ebenaceae); <i>Cercis</i> (Fabaceae); <i>Castanea, Quercus</i> (Fagaceae); <i>Carya, Juglans</i> (Juglandaceae); <i>Tilia</i> (Malvaceae); <i>Fraxinus</i> (Oleaceae); <i>Platanus</i> (Platanaceae); <i>Amelanchier, Crataegus, Cydonia, Malus, Prunus, Sorbus</i> (Rosaceae); <i>Populus, Salix</i> (Salicaceae); <i>Acer</i> (Sapindaceae); <i>Ulmus</i> (Ulmaceae)
<i>Chrysobothris igniventris</i> Reitter, 1895	Palearctic	Nearctic	Intercepted	<i>Larix, Pinus</i> (Pinaceae)
<i>Chrysobothris indica</i> Castelnau & Gory, 1837	Indomalayan	Oceanian	Established	<i>Terminalia</i> (Combretaceae); <i>Shorea</i> (Dipterocarpaceae); <i>Acacia</i> (Fabaceae); <i>Myristica</i> (Myristicaceae); <i>Mimusops</i> (Sapotaceae)
<i>Chrysobothris knulli</i> Nelson, 1975	Nearctic	Nearctic	Established	<i>Acacia</i> (Fabaceae)

Species	Biogeographic realm		Status	Plant host genera
	origin	introduction		
<i>Chrysobothris mali</i> Horn, 1886	Nearctic	Nearctic	Intercepted	<i>Alnus, Betula, Corylus</i> (Betulaceae); <i>Arbutus, Arctostaphylos</i> (Ericaceae); <i>Pickeringia, Prosopis, Wisteria</i> (Fabaceae); <i>Fagus, Quercus</i> (Fagaceae); <i>Ribes</i> (Grossulariaceae); <i>Juglans</i> (Juglandaceae); <i>Persea</i> (Lauraceae); <i>Liriodendron</i> (Magnoliaceae); <i>Ficus</i> (Moraceae); <i>Eucalyptus</i> (Myrtaceae); <i>Platanus</i> (Platanaceae); <i>Ceanothus, Rhamnus</i> (Rhamnaceae); <i>Adenostoma, Cercocarpus, Cotoneaster, Crataegus, Cydonia, Malus, Oemleria, Photinia, Prunus, Pyracantha, Pyrus, Raphiolepis, Rosa, Rubus, Sorbus</i> (Rosaceae); <i>Populus, Salix</i> (Salicaceae); <i>Acers, Aesculus</i> (Sapindaceae); <i>Ulmus</i> (Ulmaceae)
<i>Chrysobothris octocola</i> LeConte, 1858	Nearctic	Oceanian	Established	<i>Acacia, Parkinsonia, Prosopis</i> (Fabaceae); <i>Prunus</i> (Rosaceae); <i>Salix</i> (Salicaceae)
<i>Chrysobothris pupureoplagiata</i> Scheaffer, 1904	Nearctic	Nearctic	Intercepted	<i>Canotia</i> sp. (Celasteraceae), <i>Psorothamnus</i> (Fabaceae)
<i>Chrysobothris quadriimpressa</i> Gory & Laporte, 1837	Nearctic	Nearctic	Neonative	<i>Liquidambar</i> (Altaginaceae); <i>Quercus</i> (Fagaceae); <i>Juglans</i> (Juglandaceae); <i>Sapindus</i> (Sapindaceae)
<i>Chrysobothris rotundicollis</i> Gory & Laporte, 1837	Nearctic	Neotropical	Unclear	<i>Ebenopsis</i> (Fabaceae); <i>Larix, Pinus</i> (Pinaceae)
<i>Chrysobothris rugosiceps</i> Melsheimer, 1845	Nearctic	Nearctic	Neonative	<i>Castanea, Quercus</i> (Fagaceae)
<i>Chrysobothris sexpunctata</i> , Fabricius 1801	Neotropical	Neotropical	Established	Not available
<i>Chrysobothris superba</i> Deyrolle, 1864	Australasian	Paleartic	Intercepted	Not available
<i>Chrysobothris tranquebarica</i> (Gmelin, 1790)	Neotropical	Nearctic	Unclear	<i>Casuarina</i> (Casuarinaceae); <i>Conocarpus</i> (Combretaceae); <i>Cassia</i> (Fabaceae); <i>Pinus</i> (Pinaceae); <i>Rhizophora</i> (Rhizophoraceae)
<i>Chrysobothris trinervia</i> (Kirby, 1837)	Nearctic	Nearctic	Intercepted	<i>Larix, Picea, Pinus, Pseudotsuga</i> (Pinaceae)
<i>Anilara hoscheki</i> Obenberger, 1916	Australasian	Paleartic	Intercepted	Not available
<i>Melanophila consupta</i> LeConte, 1857	Nearctic	Oceanian	Non-native	<i>Calocedrus</i> (Cupressaceae); <i>Eucalyptus</i> (Myrtaceae); <i>Pinus Pseudotsuga</i> (Pinaceae)
<i>Phaenops cyanea</i> (Fabricius, 1775)	Paleartic	Nearctic	Intercepted	<i>Abies, Larix, Pinus</i> (Pinaceae)
<i>Phaenops drummondi</i> (Kirby, 1837)	Nearctic	Nearctic, Paleartic	Intercepted	<i>Abies, Cedrus, Larix, Picea, Pseudotsuga</i> (Pinaceae)
<i>Trachypterus picta decostigma</i> (Fabricius, 1787)	Paleartic	Neotropical	Established	<i>Populus, Salix</i> (Salicaceae)
<i>Nascio vetusta</i> (Boisduval, 1835)	Australasian	Australasian	Intercepted	<i>Eucalyptus, Metrosideros</i> (Myrtaceae); <i>Xanthorrhoea</i> (Asphodelaceae)

With respect to the 43 cases where the buprestids were apparently only intercepted, the Buprestinae had the highest number of interceptions worldwide (28), which included 24 species. The most commonly intercepted genus was *Chrysobothris* (14 species), followed by *Buprestis* (6 species). There were 6 cases of intercepted Agrilinae, involving 4 species of *Agrilus* and 1 *Coraebus*. For both Chrysochroinae and Polycestinae there were multiple single species interceptions. For 28 species among Agrilinae, Buprestinae, Chrysochroinae and Polycestinae it was not possible to assign their status to any of the existing categories; therefore, they were classified as “unclear.” We recognize that many more species of Buprestidae have been intercepted at ports throughout the world, but in almost all cases these datasets are not available to the public and therefore could not be considered in our paper.

Table 3. Subfamily Chrysochroinae: species list, biogeographic realms concerned, status, and larval host plants.

Species	Biogeographic realm		Status	Plant host genera
	origin	introduction		
<i>Chalcophora angulicollis</i> (LeConte, 1857)	Nearctic	Nearctic, Palearctic	Unclear	<i>Abies, Pinus, Pseudotsuga</i> (Pinaceae)
<i>Chalcophora japonica</i> (Gory, 1840)	Palearctic	Nearctic	Intercepted	<i>Pinus</i> (Pinaceae)
<i>Chalcophora virginiana</i> (Drury, 1770)	Nearctic	Neotropical, Palearctic	Unclear	<i>Taxodium</i> (Cupressaceae); <i>Pinus</i> (Pinaceae)
<i>Cyphogastra foveicollis</i> (Boisduval, 1835)	Australasian	Palearctic	Intercepted	Not available
<i>Dicerca moesta</i> (Fabricius, 1794)	Palearctic	Nearctic, Palearctic	Intercepted, Unclear	<i>Abies, Pinus, Picea</i> (Pinaceae)
<i>Dicerca furcata</i> (Thunberg, 1787)	Palearctic	Australasian	Intercepted	<i>Betula</i> (Betulaceae)
<i>Dicerca tuberculata</i> (Laporte & Gory, 1837)	Nearctic	Neotropical	Non-native	<i>Tsuga</i> (Pinaceae)
<i>Euchroma gigantea</i> (Linnaeus, 1758)	Neotropical	Neotropical	Unclear	<i>Ceiba, Pachira, Pseudobombax</i> (Malvaceae)
<i>Lampetis bahamica</i> Fisher, 1925	Neotropical	Neotropical	Intercepted	Not available
<i>Lampetis corruscans</i> (Carter, 1924)	Australasian	Australasian	Unclear	Not available
<i>Lampetis fastuosa</i> (Fabricius, 1775)	Australasian	Australasian	Unclear	<i>Areca</i> (Arecaceae); <i>Acacia</i> (Fabaceae); <i>Eucalyptus</i> (Myrtaceae); <i>Tectona</i> (Lamiaceae)
<i>Lamprodila festiva</i> (Linnaeus, 1767)	Palearctic	Palearctic	Neonative	<i>Callitris, Chamaecyparis, Cupressus, Juniperus, Platycladus, Tetraclinis, Thuja</i> (Cupressaceae); <i>Ziziphus</i> (Rhamnaceae); <i>Tamarix</i> (Tamaricaceae)
<i>Lamprodila vivata</i> (Lewis, 1893)	Palearctic	Nearctic	Intercepted	<i>Cryptomeria, Chamaecyparis, Juniperus</i> (Cupressaceae)
<i>Sphenoptera jugoslavica</i> Obenberger, 1926	Palearctic	Nearctic	Intentionally introduced	<i>Centaurea</i> (Asteraceae)
<i>Steraspis squamosa</i> (Klug, 1829)	Afrotropical, Palearctic	Palearctic	Established, Neonative	<i>Tamarix</i> (Tamaricaceae)

**Table 4.** Subfamily Polycestinae: species list, biogeographic realms concerned, status, and larval host plants.

Species	Biogeographic realm		Status	Plant host genera
	origin	introduction		
<i>Acmaeodera bipunctata</i> (Olivier, 1790)	Palearctic	Palearctic	Neonative	<i>Euphorbia</i> (Euphorbiaceae); <i>Juniperus, Thuja</i> (Cupressaceae); <i>Ficus</i> (Moraceae); <i>Abies, Cedrus, Larix, Pinus</i> (Pinaceae)
<i>Acmaeodera flavomarginata</i> (Gray, 1832)	Nearctic, Neotropical	Neotropical	Established	<i>Acacia, Prosopis</i> (Fabaceae); <i>Diospyros</i> (Ebenaceae)
<i>Acmaeodera neoneglecta</i> Fisher, 1949	Nearctic	Nearctic	Intercepted	<i>Acacia, Ebenopsis, Leucaena, Prosopis, Sophora</i> (Fabaceae); <i>Carya</i> (Juglandaceae); <i>Ulmus</i> (Ulmaceae)
<i>Prospheres aurantiopictus</i> (Laporte & Gory, 1837)	Australasian	Australasian	Established	<i>Araucaria</i> (Araucariaceae); <i>Pinus</i> (Pinaceae)
<i>Ptosima undecimmaculata</i> (Herbst, 1784)	Palearctic	Nearctic	Intercepted	<i>Mangifera</i> (Anacardiaceae); <i>Ceratonia</i> (Fabaceae); <i>Crataegus, Malus, Prunus, Pyrus</i> (Rosaceae); <i>Citrus</i> (Rutaceae); <i>Vitis</i> (Vitaceae)

Among all the taxa investigated, 22 species were considered as neonatives. There were 10 Agrilinae (9 *Agrilus* and 1 *Coraebus*); 9 Buprestinae (2 *Anthaxia*, 1 *Cobosina*, 3 *Buprestis*, and 3 *Chrysobothris*); 2 Chrysochroinae (1 *Steraspis* and 1 *Lamprodila*), and 1 Polycestinae (1 *Acmaeodera*). Neonative species were recorded almost exclusively in the Northern Hemisphere, with 15 species in the Palearctic and 6 in the

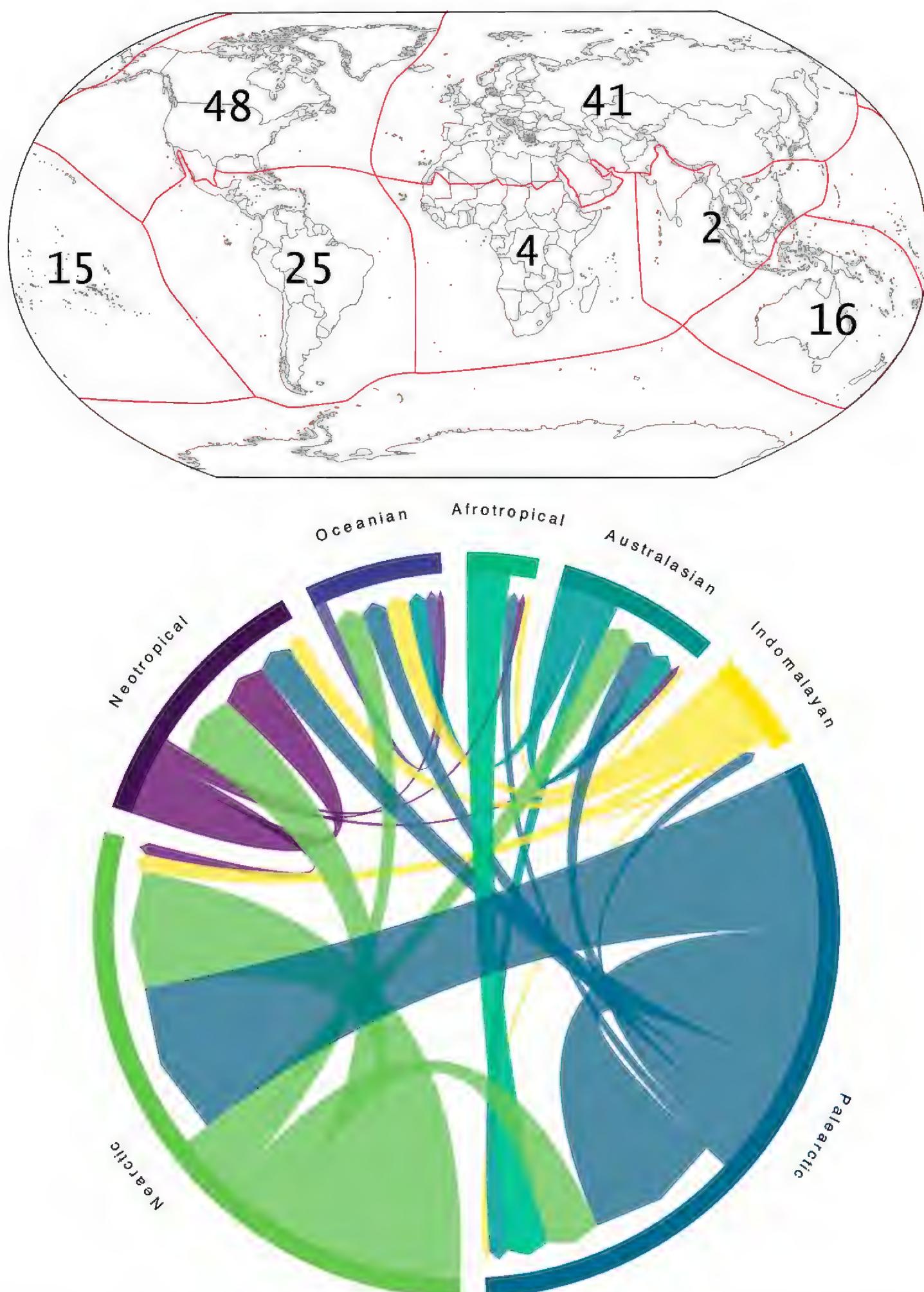


Figure 1. World map illustrating the number of introduced species of Buprestidae within and between biogeographic realms (above) and graphical representation of the exchanges (below), with the thickness of the arrows directly proportional to the number of introduction events. The length of the colored arc of each realm corresponds to the total number of introduced species, either in or out.

Table 5. Comparison between buprestid introductions within and between the Nearctic and Palearctic realms, with details on the number of species within each genus.

within Palearctic	within Nearctic	Palearctic to Nearctic	Nearctic to Palearctic
9 <i>Agrilus</i>	9 <i>Chrysobothris</i>	12 <i>Agrilus</i> (one species intentionally introduced)	3 <i>Buprestis</i>
4 <i>Buprestis</i>	6 <i>Agrilus</i>		2 <i>Chalcophora</i>
3 <i>Anthaxia</i>	2 <i>Buprestis</i>	3 <i>Buprestis</i>	1 <i>Agrilus</i>
2 <i>Coraebus</i>	1 <i>Acmaeodera</i>	2 <i>Trachys</i>	1 <i>Chrysobothris</i>
1 <i>Acmaeodera</i>	1 <i>Chalcophora</i>	1 <i>Anthaxia</i>	1 <i>Phaenops</i>
1 <i>Chrysobothris</i>	1 <i>Phaenops</i>	1 <i>Chalcophora</i>	1 <i>Trachykele</i>
1 <i>Dicerca</i>		1 <i>Chrysobothris</i>	
1 <i>Steraspis</i>		1 <i>Dicerca</i>	
1 <i>Lamprodila</i>		1 <i>Lamprodila</i>	
		1 <i>Phaenops</i>	
		1 <i>Ptosima</i>	
		1 <i>Sphenoptera</i>	
		(intentionally introduced)	

Nearctic realm. *Agrilus* was the most represented genus in the Palearctic with 7 species, while *Chrysobothris* was the most represented genus in the Nearctic with 3 species. A single species of *Cobosina* was the only example of a neonative taxon in the Neotropic realm.

All 13 cases of invasive buprestids are species of Agrilinae and Buprestinae. These species became invasive once introduced to the Nearctic, Oceanian and Neotropical realms. There were 6 species of invasive Agrilinae (5 *Agrilus* and 1 *Aphanistichus*), and only two invasive Buprestinae in the genera *Belionota* and *Chrysobothris*.

Six cases of intentionally introduced taxa were found, representing 4 species in the genera *Agrilus* (Agrilini), *Sphenoptera* (Sphenopterini), *Hylaeogena* and *Lius* (Tracheini). These species were introduced into the Nearctic, Afrotropical, and Australasian realms.

Larval host plants

The analysis of larval host plants for all Buprestidae introduced worldwide identified 158 different plant genera within 70 families (3 Gymnosperms and 67 Angiosperms), with only a few introduced buprestids without host information (Tables 1–4). The exotic Buprestidae included sets of species with wide variation in the range of their larval hosts, varying from highly polyphagous on non-phylogenetically related plant families to monophagous on a single plant genus. Larval host specificity (i.e., monophagous, oligophagous and polyphagous) of introduced Buprestidae is equally distributed among the subfamilies (Kruskal-Wallis chi-squared = 1.2007, df = 2, *p*-value = 0.5486) (Table 6).

The larval host families most represented were Pinaceae (60 host records), Rosaceae (52), Fabaceae (49), Fagaceae (36), and Cupressaceae (24), which together accounted for 52% of all host records (Table 7). Considering introductions within and between biogeographic realms, it emerged that the most common genera of host plants varied greatly among world biogeographic realms, both in abundance and diversity (Table 8).

Table 6. Number of introduced species with different levels of larval host-use specialization by buprestid subfamilies.

	Monophagous	Oligophagous	Polyphagous	Unknown
Agrilinae	13	9	17	5
Buprestinae	11	11	20	8
Chrysochroinae	5	4	3	3
Polycestinae	0	0	6	0
Total	29	24	46	16

Table 7. Summary table of the main plant families and genera exploited as larval host plants by introduced Buprestidae by subfamily. Numbers between parenthesis refers to the number of records, not distinct species.

Plant Families	Plant Genera	Buprestid subfamilies	Buprestid genera
Pinaceae (60)	<i>Pinus</i> (27), <i>Abies</i> (8), <i>Picea</i> (8), <i>Larix</i> (7)	Buprestinae (45), Chrysochroinae (9), Polycestinae (4), Agrilinae (1)	<i>Buprestis</i> (21), <i>Chrysobothris</i> (10), <i>Phaenops</i> (8), <i>Chalcophora</i> (5)
Rosaceae (52)	<i>Prunus</i> (9), <i>Malus</i> (7), <i>Sorbus</i> (7), <i>Pyrus</i> (5)	Buprestinae (30), Agrilinae (15), Polycestinae (7)	<i>Chrysobothris</i> (30), <i>Agrilus</i> (10), <i>Ptosima</i> (4), <i>Acmaeoderella</i> (3)
Fabaceae (49)	<i>Acacia</i> (9), <i>Prosopis</i> (6), <i>Ebenopsis</i> (4), <i>Leucaena</i> (3)	Buprestinae (31), Polycestinae (14),	<i>Chrysobothris</i> (29), <i>Acmaeodera</i> (7), <i>Acmaeoderella</i> (6), <i>Agrilus</i> (3)
Fagaceae (35)	<i>Quercus</i> (18), <i>Castanea</i> (11), <i>Fagus</i> (6)	Agrilinae (20), Buprestinae (13), Polycestinae (2)	<i>Agrilus</i> (17), <i>Chrysobothris</i> (11), <i>Coraebus</i> (3)
Cupressaceae (23)	<i>Juniperus</i> (5), <i>Thuja</i> (4)	Chrysochroinae (11), Buprestinae (10), Polycestinae (2)	<i>Lamprodila</i> (10), <i>Trachykele</i> (5), <i>Buprestis</i> (2), <i>Acmaeodera</i> (2)
Betulaceae (18)	<i>Corylus</i> (6), <i>Betula</i> (4), <i>Alnus</i> (3)	Buprestinae (9), Agrilinae (8), Chrysochroinae (1)	<i>Chrysobothris</i> (9), <i>Agrilus</i> (7)
Salicaceae (16)	<i>Salix</i> (9), <i>Populus</i> (7)	Buprestinae (10), Agrilinae (5), Polycestinae (1)	<i>Chrysobothris</i> (7), <i>Agrilus</i> (4), <i>Trachypteris</i> (2)

Discussion

The low introduction rate, 0.76% compared for example to the 2.17% out of ~ 6000 taxa of Curculionidae Scolytinae (Lantschner et al. 2020), indicates a general low propensity for Buprestidae to be introduced by humans, either directly or indirectly. In support of this contention is the high number of single buprestid introductions (i.e., one species introduced only once and only in a single biogeographic realm), with respect to the total number of introduction events. In addition, the invasiveness does not seem to be linked to larval host plant preferences, as introduced species are included in all feeding guilds (monophagous, oligophagous, and polyphagous).

The genera *Agrilus* (Agrilinae: Agrilini), *Buprestis* (Buprestinae: Buprestini), and *Chrysobothris* (Buprestinae: Chrysobothrini) would seem to be more predisposed to introduction events than other genera, possibly owing to both their morphological and biological traits. *Agrilus* are generally small in size and univoltine (Solomon 1995; Chamorro et al. 2015). They infest mostly live plants and signs of their presence are difficult to detect prior to adult emergence and host dieback. Therefore, several *Agrilus* species have likely been moved over time through trade of live plants, such as ornamentals or nursery stock, as well as through domestic and international movements

Table 8. Summary table of the most common plant genera exploited as larval host plants by buprestid species introduced either within or between biogeographic realms.

Origin – Introduction realm	Most common larval host plant genera exploited by those species with a narrow host range
Afrotropical – Palearctic	Angiosperms: <i>Acacia</i> , <i>Ceratonia</i> , <i>Tamarix</i>
Australasian – Australasian	Angiosperms: <i>Eucalyptus</i>
Australasian – Oceanian	Angiosperms: <i>Citrus</i>
Australasian – Palearctic	Angiosperms: <i>Anacardium</i> , <i>Casuarina</i> , <i>Ceiba</i> , <i>Delonix</i> , <i>Hopea</i> , <i>Mangifera</i> , <i>Pithecellobium</i>
Indomalayan – Afrotropical	Angiosperms: <i>Anacardium</i> , <i>Casuarina</i> , <i>Ceiba</i> , <i>Delonix</i> , <i>Hopea</i> , <i>Mangifera</i> , <i>Pithecellobium</i>
Indomalayan – Australasian	Angiosperms: <i>Anacardium</i> , <i>Casuarina</i> , <i>Ceiba</i> , <i>Delonix</i> , <i>Hopea</i> , <i>Mangifera</i> , <i>Pithecellobium</i>
Indomalayan – Palearctic	Angiosperms: <i>Citrus</i>
Indomalayan – Nearctic	Angiosperms: <i>Albizia</i> , <i>Anacardium</i> , <i>Casuarina</i> , <i>Ceiba</i> , <i>Delonix</i> , <i>Hopea</i> , <i>Mangifera</i> , <i>Pithecellobium</i> , <i>Saccharum</i> , <i>Tripsacum</i>
Indomalayan – Neotropical	Angiosperms: <i>Anacardium</i> , <i>Casuarina</i> , <i>Ceiba</i> , <i>Delonix</i> , <i>Hopea</i> , <i>Mangifera</i> , <i>Pithecellobium</i> , <i>Saccharum</i> , <i>Tripsacum</i>
Indomalayan – Oceanian	Angiosperms: <i>Citrus</i>
Nearctic – Australasian	Gymnosperms: <i>Pinus</i>
Nearctic – Nearctic	Angiosperms: <i>Acacia</i> , <i>Juglans</i> , <i>Prosopis</i> , <i>Sapindus</i> , <i>Ulmus</i>
Nearctic – Oceanian	Angiosperms: <i>Amelanchier</i> , <i>Carya</i> , <i>Prosopis</i> , <i>Prunus</i> , <i>Salix</i>
Nearctic – Palearctic	Gymnosperms: <i>Pinus</i> , <i>Pseudotsuga</i>
Nearctic – Neotropical	Gymnosperms: <i>Pinus</i>
Neotropical – Afrotropical	Angiosperms: <i>Dolichandra</i>
Neotropical – Australasian	Angiosperms: <i>Dolichandra</i>
Neotropical – Nearctic	Gymnosperms: <i>Pinus</i>
Neotropical – Neotropical	Angiosperms: <i>Acacia</i> , <i>Ceiba</i> , <i>Diospyros</i> , <i>Ebenopsis</i> , <i>Leucaena</i> , <i>Pachira</i> , <i>Prosopis</i> , <i>Pseudobombax</i>
Neotropical – Oceanian	Angiosperms: <i>Miconia</i> , <i>Tibouchina</i>
Palearctic – Afrotropical	Gymnosperms: <i>Picea</i> , <i>Pinus</i>
Palearctic – Australasian	Angiosperms: <i>Castanea</i> , <i>Fagus</i> , <i>Populus</i> , <i>Quercus</i> , <i>Tilia</i> <i>Ulmus</i>
Palearctic – Indomalayan	Gymnosperms: <i>Larix</i> , <i>Picea</i> , <i>Pinus</i>
Palearctic – Nearctic	Angiosperms: <i>Salix</i> Gymnosperms: <i>Abies</i> , <i>Larix</i> , <i>Picea</i> , <i>Pinus</i>
Palearctic – Neotropical	Gymnosperms: <i>Picea</i> , <i>Pinus</i>
Palearctic – Oceanian	Angiosperms: <i>Citrus</i>
Palearctic – Palearctic	Angiosperms: <i>Castanea</i> , <i>Quercus</i>
Oceanian – Oceanian	Gymnosperms: <i>Abies</i> , <i>Picea</i> , <i>Pinus</i>
	Angiosperms: <i>Argemone</i> , <i>Citrus</i> , <i>Intsia</i>

of recently cut logs and manufactured wood products, especially when not debarked. The example of the emerald ash borer, *A. planipennis*, is remarkable in the number of pathways (e.g., logs, firewood, nursery stock) by which it has moved in North America (Herms and McCullough 2014; Haack et al. 2015).

By contrast to *Agrilus*, most *Buprestis* and *Chrysobothris* species have longer larval developmental periods; they can infest both living, stressed, and dead plants; and they typically tunnel in host xylem, including both sapwood and heartwood (Solomon 1995; Evans et al. 2004). As a consequence of this multi-year developmental period deep inside wood, infestations are generally difficult to detect until adult emergence. Although most species oviposit in bark cracks or under the bark, a few species can oviposit directly on exposed wood (xylem). Moreover, once larvae have entered the xylem, the presence of bark is no longer required. Therefore,

introductions of these species can result from movement of logs and milled wood products either with or without bark.

Given the relatively low number of exotic buprestids investigated and the heterogeneity of the sources consulted, it has not been possible to delineate an exact temporal trend for worldwide buprestid introductions, although it seems evident that most species were likely introduced before the 1970s, with very few ever intercepted during port surveys. This condition likely reflects the lack of strict phytosanitary regulations in the early 1900s (Eschen et al. 2015). In addition, international trade among European countries and their overseas colonies likely facilitated the movement of some species early on, as well as later during the two world wars. Examples come from *Buprestis aurulenta* Linnaeus, 1767 and *Buprestis novemmaculata* Linnaeus, 1767, two species introduced in all biogeographic realms edging the Atlantic Ocean, including Azores and Canary Islands, two important bridgeheads in the trade routes between Europe and the Americas (Steckley 1972; Crosby 1984; de Avilez Rocha 2019). Similarly, sugar cane cultivation is associated with the worldwide spread of *Aphanisticus cochinchiniae seminulum* Obenberger, 1929 (Zack et al. 2009).

In more recent times, many examples of intracontinental spread of buprestids have been reported, especially for certain species of *Agrilus*, *Anthaxia*, and *Chrysobothris* (Westcott 2005; Fägerström et al. 2009; Izzillo 2013; Orlova-Bienkowskaja and Volkovitsh 2015; Westcott et al. 2018; Curletti and Ranghino 2020). Rapid intracontinental spread probably reflects greater connectivity among trading partners as well as increased speed of transport, especially in the European Union and North America. Range expansion of some neonative species has apparently resulted from human-caused climate and environmental changes, such as for *Agrilus graminis* Kiesenwetter, 1857; *Agrilus nicolanus* Obenberger, 1924; *Buprestis dalmatina* Mannerheim, 1837; *Lamprodila festiva* (Linnaeus, 1767). In the USA, the southward and westward spread of the native birch specialist *Agrilus anxius* Gory, 1841 has been attributed to the widespread planting of ornamental birch trees in many areas outside the native range of North American birch species (Muilenburg and Herms 2012).

It is interesting to note that most neonatives have caused little damage, although there are a few exceptions often associated with the inadvertent movement of infested live plants. For example, the introduction of *Agrilus planipennis* from Eastern Asia to the Moscow area resulted in severe mortality of ash (*Fraxinus*) trees in European Russia (Orlova-Bienkowskaja 2014); however, it is also plausible that *Agrilus planipennis* could have been introduced in Moscow on ash nursery stock imported from North America (Haack et al. 2015). Another example is *Lamprodila festiva* (Linnaeus, 1767), a southern European – circum-Mediterranean species, which has expanded its distribution northward and eastward, benefiting from extensive plantings of its host plants (Cupressaceae) as ornamental plants in private and public gardens (Nitzu et al. 2016; Rabl et al. 2017; Volkovitsh and Karpun 2017; Ruicănescu and Stoica 2019). Similarly, *Agrilus mali* Matsumura, 1924, an eastern Palearctic species, has taken advantage of expanding cultivation of Rosaceae fruit trees and patches of natural forest as a springboard to spread westward in the Palearctic (Volkovitsh et al. 2020; Zhang et al. 2021; Lu et al. 2022).

Only four buprestid species have been intentionally introduced as biological control agents against invasive weeds in North America, South Africa, and Australia. *Sphenoptera jugoslavica* Obenberger, 1926 has been intentionally introduced and successfully established in the western USA where it is used to control the invasive plant *Centaurea diffusa* Lam. (Asteraceae) (Lang et al. 1998); *Agrilus hyperici* (Creutzer, 1799) was introduced in the USA and Australia where it provides efficient control of invasive *Hypericum* species (Hypericaceae); while *Hylaeogena jureceki* Obenberger, 1941 was introduced and established with different rates of success in South Africa and Australia to control the invasive plant *Dolichandra unguis-cati* (L.) L.G.Lohmann (Bignoniaceae) (King et al. 2011; Snow and Dhileepan 2014). The Neotropical *Lius poseidon* Napp, 1972 was instead intentionally introduced to Hawai'i to control the invasive *Miconia crenata* (Vahl) Michelang (Melastomataceae); however, in Hawai'i the species naturally became a biocontrol agent of another invasive plant *Chaetogastra herbacea* (DC.) P.J.F.Guim. & Michelang. (Melastomataceae) (Culliney and Nagamine 2000; Conant and Hirayama 2001; Conant et al. 2013).

Conclusion

The family Buprestidae is highly diverse with a global distribution defined by multiple abiotic and biotic factors, including human-mediated introductions. Although some biological and ecological traits, such as apparent obligate outbreeding and obligate maturation feeding for all buprestids, can serve as barriers to successful establishment, the opening of new continental and intercontinental trade routes as well as the ever-increasing volume and types of goods and plants traded increases the risk of future introductions or passive diffusion of more buprestid species. With respect to climate change and the widespread practice of introducing exotic plants for ornamental, agricultural, and forestry purposes around the world, it will be important to identify possible new introduction pathways for exotic Buprestidae along with pest risk assessments. In this regard, more research is needed on buprestid taxonomy and ecology, together with training and funding of more buprestid specialists. The development of new technologies for rapid species identification, either morphological or molecular, would be very useful for the management of this important group of plant pests, which are becoming of increasing economic importance worldwide.

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Supplementary material I

Systematic list of all Coleoptera Buprestidae introduced around the world between 1850 and 2020

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Data type: table (excel document)

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